

STUDIES IN THE HELIANTHEAE (ASTERACEAE). XII.

RE-ESTABLISHMENT OF THE GENUS SMALLANTHUS.

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In the Heliantheae subtribe Melampodiinae the genera are often well-marked and there seems to be little need to the casual observer for subtle generic distinctions. It is in this climate that the concept of Polymnia has been maintained for coarse herbs or shrubs in the subtribe having opposite leaves and ray achenes not enclosed in a bract. In the recent monograph by Wells (1965) no consideration seems to have been given to any alternative concept. The existence of the segregate genus Smallanthus of Mackenzie (1933) was scarcely noted by Wells under the synonymy of Polymnia uvedalia (L.) L. A re-evaluation shows that Smallanthus is a valid genus that should be expanded from the one species originally included to contain the majority of the species which have previously been placed in Polymnia.

The initial difference between the two genera noted in the present study and in the characterization of Mackenzie is the form of the achene. In Polymnia the achene walls are smooth without striations while Smallanthus has shallow grooves that are evident on the surface. Not mentioned by Mackenzie were the shape of the achenes, tangentially broadened and flattened with three to five distinct ribs in Polymnia, and radially thickened and laterally compressed often without distinct ribs in Smallanthus. The wall of the Smallanthus achene is also very thick with a massive layer of softer internal tissue not seen in the thin walls of Polymnia. The outer cell layer of Polymnia differs in the regular pattern of small broadly hexagonal cells more or less in rows.

Mackenzie (1933) noted as a second character the basic pinnate venation of the Polymnia leaf. The lower part of the leaf blade has at least a pair of short lobules and often has many pinnately disposed lobes. Most species of Smallanthus do have trinervate or palmately lobed leaf blades, but there are some species such as S. macvaughii and S. oaxacanus with pinnately lobed leaf blades.

A number of differences occur in addition to

those mentioned by Mackenzie. Polymnia does not have the distinct whorl or near whorl of outer involucre bracts which is one of the most prominent features of Smallanthus. Polymnia has glands on the thin anther appendages while such glands are apparently lacking on the indurated anther appendages of Smallanthus. The hairs on the corollas of Polymnia including the numerous hairs of the tube of the rays are thin-walled and blunt-tipped. The corolla hairs of Smallanthus seem particularly firm and sharp-pointed in contrast. The lobes of the disk corollas of Polymnia have a feature lacking in not only Smallanthus but other genera of the Heliantheae, a series of short multicellular hairs along the margin many of which are on the inside surface. The various cytological studies of the species are reviewed by Wells (1965). The two species of Polymnia have a number of $n=15$. Species of Smallanthus with the exception of some dubious or polyploid counts seem to have $n=16$ with one count of $n=17$.

Clear evidence of phyletic distance between Smallanthus and Polymnia is available, but exact relationships remain in doubt for three reasons. The first is that numerous differences also occur between both genera and all others with which they might be compared, the second is the apparent artificiality of the subtribe Melampodiinae as was partially noted in the study by Stuessy (1973), and the third is the problem of interpreting the character of striations on the achene. The achene striation has been of great value in delimiting other subtribes of the Heliantheae, but it does not correlate well with other characters in the Melampodiinae. It is not even certain that the poorly differentiated undulating structure in Smallanthus is equivalent to striations as seen in other genera of the tribe. The latter are usually not evident on the surface of the achene but have clear cell differentiation internally. Melampodium has regular striations in the achene wall and might be closely related to Smallanthus, but Acanthospermum which has been placed close to Melampodium has no regular striations. Espeletia usually lacks striations which would be more like Polymnia, but the achene shape is nearer Smallanthus. In all the comparisons the impression persists that true Polymnia is the most isolated among the genera of the subtribe. It is clear that the characters on which relationships in the Melampodiinae have been based need complete re-evaluation, and this can be done properly only by considering Polymnia and Smallanthus as separate entities.

The genus Polymnia is typified by P. canadensis L. which was interpreted broadly by Wells (1965) to include P. variabilis Poiret, the type species of Polymniastrum Lam. The latter was based on material in which the ray corollas lacked a limb. The only other species in the genus is P. laevigata Beadle. Both species are restricted to eastern North America. The remaining species treated by Wells fall into the genus Smallanthus with the addition of one new species, one species more recently described by Wells (1967), and one species resurrected from synonymy.

Smallanthus Mackenzie in Small, Man. Southeast. Fl. 1406. 1933. Type species: Osteospermum uvedalium L.

Smallanthus apus (Blake) H. Robinson, comb. nov.
Polymnia apus Blake, Contr. U.S. Nat. Herb. 22: 604. 1924. Mexico.

Smallanthus connatus (Spreng.) H. Robinson, comb. nov.
Gymnolomia connatum Spreng., Syst. Veg. 3: 610. 1826. Uruguay, Brasil, Paraguay, Argentina.

Smallanthus fruticosus (Benth.) H. Robinson, comb. nov.
Polymnia fruticosa Benth., Pl. Hartw. 209. 1845. Ecuador, Colombia, Peru.

Smallanthus glabratus (DC.) H. Robinson, comb. nov.
Polymnia glabrata DC., Prodr. 5: 515. 1836. Chile, Ecuador, Peru.

Smallanthus jelskii (Hieron.) H. Robinson, comb. nov.
Polymnia jelskii Hieron., Bot. Jahrb. 36: 484. 1905. Peru. The double corollas of the rays cited by Wells (1965) are an unreliable character, but the species can be distinguished from the closely related S. pyramidalis by the very short limbs of the ray corollas and by the finer denser hairs on the pedicels and paleae.

Smallanthus latisquamus (Blake) H. Robinson, comb. nov.
Polymnia latisquama Blake, Journ. Wash. Acad. Sci. 16: 421. 1926. Costa Rica. The species was placed in the synonymy of S. quichensis by Wells (1965) but it has much larger heads on stout pedicels and the upper leaf surface is not or scarcely scabrous.

Smallanthus lundellii H. Robinson, sp. nov.
Plantae herbaceae vel suffrutescentes 1 m altae?
Folia opposita, petiolis 0.5-1.5 cm longis non alatis;

laminae ovato-ellipticae usque ad 20 cm longae et 13 cm latae base anguste cuneatae margine utrinque plerumque 2-3-angulato-dentatae et multo remote mucronato-denticulatae apice anguste breviter acuminatae in quadrante inferiore valde trinervatae supra nigro-virides sparse scabridae subtus pallido-virides in nervis et nervulis pilosae. Inflorescentiae paucicapitatae saepe subscaposae, pedicellis 3.0-3.5 cm longis dense hirtellis et stipitato-glanduliferis. Capitula late campanulata; squamae involucri exteriores 5 base breviter connatae subrotundatae 6-12 mm longae et latae margine multo crenatae et sparse pilosulae apice obtusae intus puberulis extus minute puberulae et in medio breviter pilosae; bractee interiores ca. 10 late obovatae ca. 5 mm longae et 4 mm latae margine integrae apice obtusae extus dense puberulae et breviter stipitato-glanduliferae; flores radii ca. 10; corollae flavae, tubis ca. 2 mm longis dense hirtellis, limbis oblongis ca. 13 mm longis et 7.5 mm latis apice breviter tridentatis; flores disci ca. 100; corollae flavae 6.0-6.5 mm longae, tubis ca. 1 mm longis glabris, lobis ca. 1 mm longis et latis extus paucae valde scabridis; filamenta in parte superiore ca. 0.4 mm longa; thecae antherarum nigrescentes ca. 1.8 mm longae; appendices antherarum ovatae 0.5-0.6 mm longae ca. 0.4 mm latae; achaenia radii subglobosa vel obovata 4.0-4.5 mm longa nigra; pappus nullus. Grana pollinis ca. 32 μ in diam.

TYPE: GUATEMALA: Baja Verapaz: Union Barrios, on the Salama-Coban Road, south of km. 147, in high forest on hill. Coarse herb, rays of flowers yellow. Feb. 5, 1975. C.L. Lundell & E. Contreras 18916 (Holotype US, isotypes in Lundell Herbarium at Dallas).

Smallanthus lundellii has the petiole unwinged below the cuneate base of the leaf blade and it would key to S. quichensis in treatments that emphasize that character. The new species differs from both S. quichensis and the related S. latisquamus by the more angulate lower leaves and the densely pubescent pedicels. The species is named for the collector, Dr. Cyrus L. Lundell, who has donated the holotype for deposit in the U.S. National Herbarium.

Smallanthus maculatus (Cav.) H. Robinson, comb. nov.

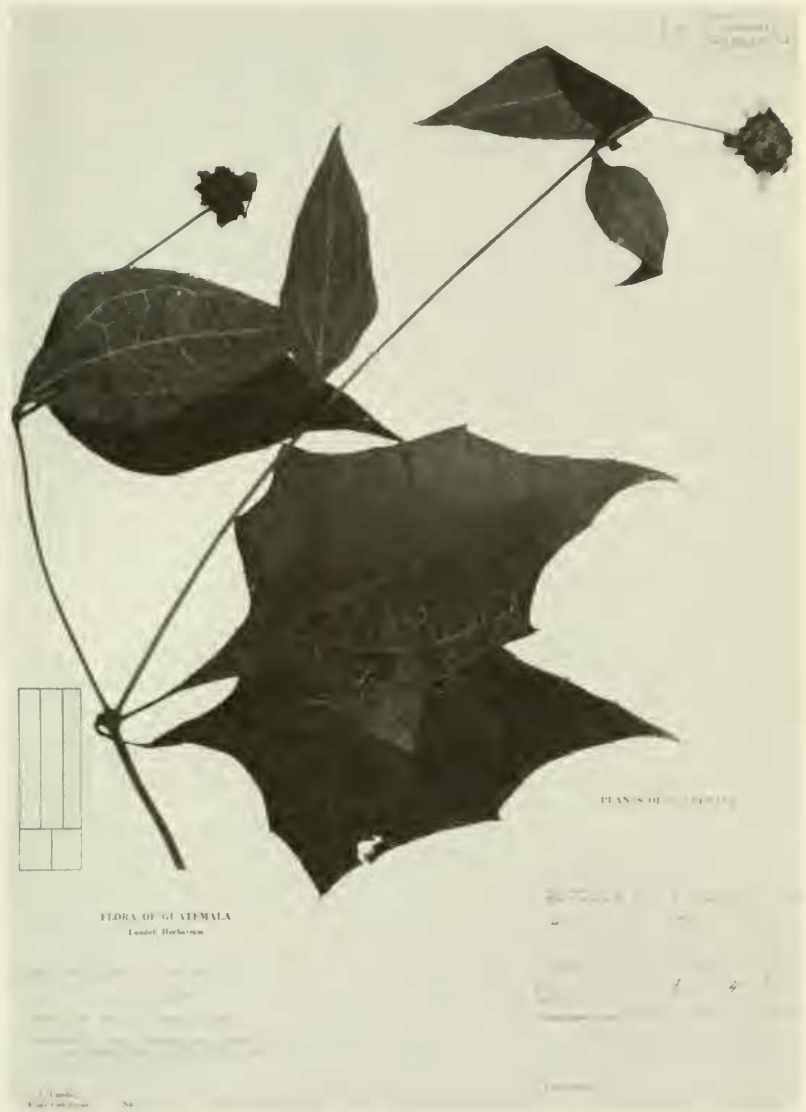
Polymnia maculata Cav., Icon. Pl. 3: 14. 1794.
Mexico, Central America. 1795.

Smallanthus macvaughii (Wells) H. Robinson, comb. nov.

Polymnia macvaughii Wells, Brittonia 19: 392. 1967.
Mexico.

- Smallanthus meridensis (Steayerm.) H. Robinson, comb. nov. Polymnia meridensis Steayerm., Fieldiana, Bot. 28: 667. 1953. Venezuela, Colombia.
- Smallanthus microcephalus (Hieron.) H. Robinson, comb. nov. Polymnia microcephala Hieron., Bot. Jahrb. 29: 33. 1900. Ecuador.
- Smallanthus oaxacanus (Sch. Bip. ex Klatt) H. Robinson, comb. nov. Polymnia oaxacana Sch. Bip. ex Klatt, Leopoldina 23: 89. 1887. Mexico, Central America.
- Smallanthus parviceps (Blake) H. Robinson, comb. nov. Polymnia parviceps Blake, Contr. U.S. Nat. Herb. 22: 604. 1924. Peru, Bolivia.
- Smallanthus pyramidalis (Triana) H. Robinson, comb. nov. Polymnia pyramidalis Triana, Ann. Sci. Nat. ser IV, 9: 40. 1858. Colombia, Venezuela, Ecuador.
- Smallanthus quichensis (Coult.) H. Robinson, comb. nov. Polymnia quichensis Coult., Bot. Gaz. 20: 48. 1895. Guatemala.
- Smallanthus riparius (H. B. K.) H. Robinson, comb. nov. Polymnia riparia H. B. K., Nov. Gen. et Sp. ed folio 4: 222. 1818. Colombia, Venezuela, Peru, Ecuador, Bolivia, Guatemala.
- Smallanthus siegesbeckius (DC.) H. Robinson, comb. nov. Polymnia siegesbeckia DC., Prodr. 5: 516. 1836. Brazil, Paraguay, Bolivia, Peru.
- Smallanthus sonchifolius (Poepp. & Endl.) H. Robinson, comb. nov. Polymnia sonchifolia Poepp. & Endl., Nov. Gen. et Sp. Pl. 3: 47. 1845. Peru, Ecuador, Bolivia.
- Smallanthus suffruticosus (Baker) H. Robinson, comb. nov. Melampodium suffruticosum Baker in Mart., Fl. Bras. 6 (3): 162. 1884. Venezuela.
- Smallanthus uvedalius (L.) Mackensie in Small, Man. Southeast. Fl. 1406. 1933. Osteospermum uvedalia L., Sp. Pl. 2: 923. 1753.

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in J. K. Small, *Manual of the Southeastern Flora*.
1307, 1406.
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Subtribe *Melampodiinae* (*Compositae*, *Heliantheae*).
Contr. Gray Herb. Harvard Univ. 203: 65-80.
- Wells, J. R. 1965. A taxonomic study of Polymnia
(*Compositae*). *Brittonia* 17: 144-159.
- _____. 1967. A new species of Polymnia (*Compositae*:
Heliantheae) from Mexico. *Brittonia* 19: 391-394.



Smallanthus lundellii H. Robinson, Holotype,
United States National Herbarium. Photos by Victor E.
Krantz, Staff Photographer, National Museum of Natural
History.